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The Formal Model for *Noctua pronuba* (Lepidoptera, Noctuidae) representing a typical agricultural-landscape night-flying moth species for pesticide risk assessment

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Abstract

Nocturnal lepidopteran pollinators face pesticide exposure risks in agricultural landscapes, yet lack adequate risk assessment frameworks compared to diurnal species. We present a formal model description for *Noctua pronuba* within the Animal Landscape and Man Simulation System (ALMaSS), providing the first comprehensive agent-based framework for assessing the impacts of pesticides on nocturnal moth pollinators. The model integrates temperature-dependent development using Lobry–Rosso–Flandrois thermal performance curves, stage-specific behaviours including photoperiod-triggered reproductive diapause and nocturnal foraging, and realistic dispersal capabilities up to 11 km. Three pesticide exposure pathways (dietary intake, contact, and overspray) enable risk assessment across all life stages, while multiple mortality sources capture natural population regulation through parasitism, disease, and density-dependent processes. Model parameterisation primarily draws on comprehensive historical studies of *N. pronuba*, supplemented by data from related noctuid species where gaps exist. The framework's modular design enables adaptation to other nocturnal lepidopteran species by adjusting parameters. We explicitly define the model's applicability domain as temperate European agricultural systems and acknowledge key limitations, including the exclusion of evolutionary responses and sublethal pesticide effects. This spatially explicit, behaviorally realistic framework provides regulators with a practical tool for comparing relative pesticide risks across landscape scenarios while recognising inherent uncertainties in predicting absolute population outcomes. The model addresses a critical gap in pollinator risk assessment by representing an ecologically important but understudied guild of nocturnal pollinators.

Key words: Agent-based model, ALMaSS, noctuid moth, risk assessment model

Introduction

This paper follows the formal model format (Topping et al. 2022) and describes a prototype model prior to implementation for a noctuid moth model based on the common yellow underwing, *Noctua pronuba*, and similar species with broad larval host choice and univoltine dynamics. *N. pronuba* is the type species of the moth family Noctuidae, is widespread and common in its native Palearctic

region, and is widespread and invasive in the Nearctic (Heath and Emmet 1979; Fibiger 1993; Boyes and Holland 2022). The species is sexually dimorphic and highly polymorphic and is found in many habitats, from grasslands to forests. It is typically univoltine, with adults occurring from late May to November, but most often in July and August. *N. pronuba* females lay eggs in clusters in vegetation, and larvae feed on a wide range of herbaceous plants and grasses. Adults mainly feed on nectar from flowers. There is a reasonable volume of data on this species from which to define and parameterise the model for most aspects. Much of this data derives from Singh's (1956) comprehensive PhD study. However, some areas are difficult to parameterise, such as dispersal and oviposition. Consequently, we have designed the model to be flexible, allowing us to adjust parameters as new information becomes available or to incorporate information from other similar species.

The model is designed for inclusion in ALMaSS (Animal Landscape and Man Simulation System; Topping et al. 2003; Topping and Duan 2024a, 2024b). Therefore, we rely on this system's features and adapt to the functional limitations imposed by the framework, primarily related to the level of detail in the habitat units it represents. ALMaSS provides a highly detailed landscape modelling framework at a one-meter resolution and is typically employed to simulate landscapes of 10 × 10 km, although the upper limit is set only by hardware constraints. The landscape model is dynamic, includes details of farming and pesticide applications, and provides geospatial and temporal variation in habitat type and quality.

The following sections detail the formal model development, with particular emphasis on its intended application in pesticide risk assessment in European agricultural landscapes.

Aims and purpose

The ALMaSS Noctuid Moth model is designed to represent night-flying lepidopteran pollinators in European agricultural landscapes. The initial application of the model aims to provide a representative of this group for use in a systems-based approach to regulatory risk assessment for pollinators that are directly or indirectly impacted by agrochemical use, primarily through the use of pesticides. As such, we have a specific section in the formal model for the implementation of pesticide exposure and effects. The model utilises parameter estimates for *N. pronuba* as far as possible (e.g., Singh 1956; Madge 1962), but remains generic, with a degree of flexibility in definition that allows for the representation of different species within the general group. Knowledge concerning the details of any one noctuid moth species remains more limited than that available for butterflies, such as *Pieris napi* (Topping and Duan 2025); hence, the parameter scoping is allowed to be more flexible.

Theoretical framework and modelling approach

The model is designed to represent the reproduction, mortality, development, and movement of a noctuid moth using an individual-based approach within the ALMaSS framework, tailored for potential use in pesticide regulatory environmental risk assessments for pollinators.

As with other published pollinator models in ALMaSS (Duan et al. 2022; Ziółkowska et al. 2023), we employ an agent-based modelling approach in which each moth is represented as an independent code object. At any given time, each object possesses specific characteristics, such as age, size, location, and pesticide loading, which influence its behavioural states. For instance, the moth's size is linked to its reproductive capacity.

The ALMaSS modelling environment provides a detailed spatio-temporal representation of the landscape, enabling individual moths to access the information needed to simulate their behaviour at high spatial resolution. The landscape representation and its interface to agent-based models are described in Topping and Duan (2024a). This landscape model incorporates a detailed raster land-cover map with a 1 m² spatial resolution and a habitat polygon map. Farms are represented as collections of fields, classified by farm type (e.g., cattle or arable farms), which determine the crops grown and influence pesticide use and crop management. Each farm follows a tailored management model, with crop systems represented by pluri-annual crop rotations based on the farm's crop types, arranged in an agronomically logical order.

Crop and non-crop vegetation growth is simulated daily and influenced by management practices, weather, and soil conditions. Additionally, a pollen and nectar model is implemented for flowering vegetation (Ziółkowska et al., in preparation), providing daily nectar availability per unit area for moths to forage.

All life stages of the moth are represented as individuals in the model, with their internal development and interactions with one another and the environment described in the following sections. To maximise efficiency and ease of understanding, the structure of this model is based on the *Pieris napi* model, which is currently the only other lepidopteran model in the ALMaSS system.

We aim to standardise temperature relationships as far as possible across ALMaSS models and within each model. We propose a standard framework for phenology models and note that most models of insect development rely on a thermal performance curve (TPC) to describe the relationship between development rate and temperature, as well as rate summation. Thus, maturation to the next stage occurs when development (based on the TPC and the distribution of environmental temperature) reaches a threshold. For the *P. napi* model, the Lobry–Rosso–Flandrois (LRF) TPC model was proposed to describe nonlinear growth using four parameters. The LRF model, named by Ratkowsky and Reddy (2017), was proposed to represent microbial growth (Lobry et al. 1991; Rosso et al. 1993). The four parameters represent three cardinal temperatures—the maximum temperature at which development can occur (T_{max}); the minimum development temperature (T_{min}); and the optimum development temperature (T_{opt})—and the specific growth rate at the optimum (U_{opt}). U_{opt} is independent of the three cardinal temperatures, and T is the temperature (Equation 1).

$$r(T) = u_{opt} \frac{(T - T_{max})(T - T_{min})^2}{(T_{opt} - T_{min})\left[(T_{opt} - T_{min})(T - T_{opt}) - (T_{opt} - T_{max})(T_{opt} + T_{min} - 2T)\right]} \quad \text{Equation 1}$$

We propose using the LRF model to represent development in the *N. pronuba* model, but without the benefit of the model already being parameterised by literature. The reason for this choice is the straightforward translation of the four parameters to descriptive features of the development process.

Overview of processes

Growth and development

Many of the most detailed estimates of noctuid growth and development have been obtained for pest species such as *Helicoverpa armigera* (Jallow and Matsumura 2001). For instance, *H. armigera* reared at constant temperatures did not develop from egg to adult (emergence) outside the temperature range of 17.5°C to 32.5°C. The experiment also employed an alternating-temperature treatment, which expanded the temperature range to 10–35°C. The lowest developmental thresholds of the immature stages were estimated using a linear model and ranged from 10.17°C (pupal stage) to 11.95°C (egg stage) at constant temperatures and from 1.1°C to 5.5°C at alternating temperatures. A TPC was also fitted, giving lower minimum development temperatures. Females reared under all alternating-temperature regimes laid more eggs than females reared at any constant temperature except the 25°C treatment. Extreme temperatures had negative effects. Similar developmental studies of other pest species provide comparable findings. Linear and nonlinear developmental models were used to model *H. armigera*, *Spodoptera frugiperda*, and *Busseola fusca* larval development, all showing similar results with optimum temperatures between 26°C and 30°C and upper limits from 30°C to 35°C (Jallow and Matsumura 2001; Noor-ul-Ane et al. 2018; Du Plessis et al. 2020; Jung et al. 2023; Maharjan et al. 2023). This suggests that the underlying developmental pattern is common among many noctuids and can be easily modelled.

The data for *N. pronuba* (e.g., Singh 1956; Madge 1962) are also of high quality and generally align with the pest species noted above. This suggests that within this group of moths, these relationships may be broadly similar. The upper developmental bound in *N. pronuba* is likely lower because most of the pest studies are from warmer climates to which those species are locally adapted. The data from Singh (1956) confirm this. Even in *Xestia c-nigrum*, a multivoltine species, developmental rates showed a very similar pattern to that of *N. pronuba* (Madge 1962). Overall, this suggests that the *N. pronuba* model could be easily modified to represent other similar species.

Eggs

The following summary comes from Madge (1962) for *N. pronuba*:

- The development rate of eggs at alternating temperatures was similar to that at the same stable mean temperature, except for the 10°C group, where development took much longer.
- Sub-threshold temperatures: Eggs incubated at very low temperatures (5°C and 0.8°C) did not hatch but showed some development.
- Semi-natural conditions: Nearly all eggs hatched after 12 to 13 days at a mean temperature of around 14°C in a semi-natural setting. However, when the temperature dropped below 5°C, only 4% of the eggs hatched after 5 weeks, indicating that lower temperatures significantly hindered development.

In an extensive study, Singh (1956) evaluated the time to hatch of eggs of *N. pronuba*, *Agrostis segetum*, and *Xestia c-nigrum* under different constant temperatures. Thresholds for development time were given as 7.5°C, 7.7°C, and

8.0°C, respectively. There were differences in the upper threshold between the species. *N. pronuba* failed to develop at 30°C, but both other species failed at 35°C. This indicates that similar developmental patterns are followed by these related species, but small differences in response thresholds occur.

Singh (1956) provides days-to-hatch values for temperatures ranging from 10°C to 35°C in 5-degree increments. Together with the data from Madge (1962), this information provides a solid basis for creating a TPC model for egg development in *N. pronuba*.

Larvae

According to Singh (1956), the larval period consists of two distinct phases. The first phase, from egg emergence to the cessation of feeding, marks progressive development. The second phase, the pre-pupal stage, begins when feeding stops in preparation for pupation. The normal situation is that just before the pre-pupal stage, the larvae descend into the soil, where they construct earthen cells within 3–7 cm of the surface. Under favourable conditions, caterpillars transition directly to the pupal stage with a minimal pre-pupal period. However, under unfavourable conditions, such as temperature fluctuations, the pre-pupal phase is prolonged, and feeding ceases for an extended period, causing larvae to enter a state of torpor. In the USA, this species is often referred to as the snow or winter cutworm, as feeding can commence in warm conditions during winter (Difonzo and Russell 2010; Wagner 2010).

Larval development: Summarising Madge (1962) for larval development, who studied *N. pronuba* larvae at 10°C, 15°C, 20°C, 25°C, and 27.5°C:

- 10°C: At this temperature, the total life cycle lasted about 9 months. However, due to infections, only about 10% of the larvae survived to maturity.
- 15°C: This temperature was optimal for survival, with nearly half of the original number of larvae completing their development. The life cycle at this temperature took approximately 8 months.
- 20°C: Similar to 15°C, this temperature supported a significant number of larvae completing development, but the duration was shorter, taking about 3 months.
- 25°C: At this higher temperature, only 7% of the larvae survived, and those that did complete their development within about 2 months.
- 27.5°C: No larvae survived beyond the sixth instar at this temperature, and most died shortly after hatching.

Overall, the study presents a pattern of development increasing with temperature but with an optimum for survival at around 15–20°C. By 27.5°C, a thermal survival threshold is crossed, preventing survival.

Singh (1956) performed similar experiments at additional temperatures—10°C, 15°C, 18°C, 20°C, 23°C, 25°C, and 27°C for *N. pronuba*, and 10–35°C in 5-degree increments for *A. segetum* and *X. c-nigrum*. No development occurred at 35°C. For *N. pronuba*, development still occurred at 27°C, albeit slightly faster than at 25°C. Unfortunately, mortality rates were not reported, making direct comparison with the later study by Madge (1962) impossible. However, in Singh's (1956) study, larvae exposed to temperatures of 8°C and below did not pupate, compared to 100%

pupation at 21°C. Yet, larvae at 5–8°C survived in a dormant state for 170–190 days. In the same study, the effects of photoperiod and soil moisture were investigated; however, neither factor influenced hibernation or diapause in the larvae.

Larval growth was recorded as the length of each larval stage (stages 1–7), after moulting or emergence, reaching 48 mm before the pre-pupal stage. Head capsule widths were also provided. This information can be used to assess the proportion of development time associated with each stage. Both measures fit an exponential growth curve with similar slopes (length: $y = 0.045e^{0.4735x}$, $R^2 = 0.9632$, head width: $y = 0.0618e^{0.4064x}$, $R^2 = 0.9965$). However, when examining the proportion of length gained per stage, the pattern was almost linear ($y = 0.0506x - 0.0595$, $R^2 = 0.9783$) (Table 1). This calculation suggests that we can probably assume a linear progression between instars under constant temperatures.

Table 1. Growth measures from Singh (1956) for *Noctua pronuba* larval length and head width, with calculations of the proportion of growth per larval stage.

Larval Stage	Length (mm)	Head width (mm)	Growth post Hatch (mm)		Proportion of growth	
					Length	Head)
1	2.20	0.307	0	0.000	0.00	0.00
2	4.50	0.490	2.30	0.183	0.06	0.06
3	8.00	0.750	3.50	0.260	0.10	0.08
4	13.50	1.150	5.50	0.400	0.15	0.13
5	20.00	1.700	6.50	0.550	0.18	0.17
6	30.00	2.500	10.00	0.800	0.28	0.25
7	38.00	3.500	8.00	1.000	0.22	0.31

Following development, the larvae enter a diapause state with arrested development until pupation.

Pupae

Post-diapause development has been accurately modeled using TPCs in the pea moth *Cydia nigricana* (Lepidoptera, Tortricidae) (Riemer et al. 2021). In the same study, it was concluded that there was no response to photoperiod during post-diapause development. Singh (1956) provided pupal development rates for *N. pronuba*, *A. segetum*, and *X. c-nigrum*, which varied with temperature. As with egg and larval development, *A. segetum* was very similar to *N. pronuba*, with the multivoltine *X. c-nigrum* having faster development of larvae and pupae (Singh 1956). In *N. pronuba*, no pupae developed at 35°C, but the other two species completed development at this temperature. Although not investigated in detail, no effect of photoperiod was found in *N. pronuba*. The same study, however, did not provide data on temperature-related mortality.

Implementation in the model

Three parameterisations for eggs, larvae, and pupae were fitted to the data from Singh (1956) and Madge (1962) using the LRF TPC model in the R package rTPC (Padfield et al. 2024). The resulting estimates for the models, fitted to the data, are presented in Table 2.

Table 2. Parameter estimates for the LRF thermal performance curve for *Noctua pronuba* egg developmental rate. Residual standard error: 0.007007 on 3 degrees of freedom. *** = p < 0.0001.

Parameter	Estimate	Std. Error	t-value	Pr(>|t|)
u_{opt}	0.205836	0.004768	43.17	2.74e-05 ***
T_{opt}	25.986514	0.344582	75.42	5.14e-06 ***
T_{min}	0.000000	1.328620	0.00	1
T_{max}	29.000124	0.019113	1517.30	6.31e-10 ***

For the larvae, the earlier study data from Singh (1956) were used to fit the model, except for the zero development at 27.5°C. The resulting parameter estimates for development are given in Table 3.

Unfortunately, this model does not allow us to identify the point at which each instar matures. To include this, we need an estimate of the proportion of development required for each maturation point. Since a linear response in body size measures with larval stage was observed, we will make the simplifying assumption that stage progression occurs at each 1/7 of the total development time. This estimate can be adjusted if more detailed information becomes available.

Table 3. Parameter estimates for the LRF thermal performance curve for *Noctua pronuba* larval developmental rate. Residual standard error: 0.001369 on 4 degrees of freedom. *** = p < 0.0001.

Parameter	Estimate	Std. error	t-value	Pr(>|t|)
u_{opt}	0.044481	0.004296	10.35	0.000491 ***
T_{opt}	28.970761	0.282118	102.69	5.39e-08 ***
T_{min}	0.000000	1.764163	0.00	1
T_{max}	27.500043	0.005105	5386.87	13e-15 ***

Table 4. Parameter estimates for the LRF thermal performance curve for *Noctua pronuba* pupal developmental rate. Residual standard error: 0.001301 on 3 degrees of freedom. *** = p < 0.0001.

Parameter	Estimate	Std. Error	t-value	Pr(>|t|)
u_{opt}	0.05870	0.0009605	61.11	9.65e-06 ***
T_{opt}	28.65	0.344582	75.42	5.14e-06 ***
T_{min}	0.000000	1.051	0.00	1
T_{max}	35.00	0.04176e-02	838.15	3.75e-09 ***

For pupae, fitting the LRF model to the data provided by Singh (1956) resulted in a good fit (Table 4).

The data points used, along with the fitted lines for all three life stages, are shown in Figure 1. In all cases, the fits to the parameters were highly significant, except for T_{min}, for which the estimate is highly uncertain. In the case of eggs and larvae, using a linear model, the thermal minimum was calculated to be 7.5°C and 7.0°C, respectively. In cold tolerance experiments, no development of eggs or larvae was observed below 6°C. To match observations and due to the poor fit to T_{min}, we propose that the curve be truncated at 6.0°C, below which there is no development.

For pupae, similar results were obtained in the same study, with a threshold temperature of 7–8°C. In this case, we propose truncating the curve at 7°C.

Larval hibernation and the onset of diapause seem to be linked to temperature. We will assume that growth stops below the developmental threshold of 6.0°C. Above this threshold, development will occur until pupation.

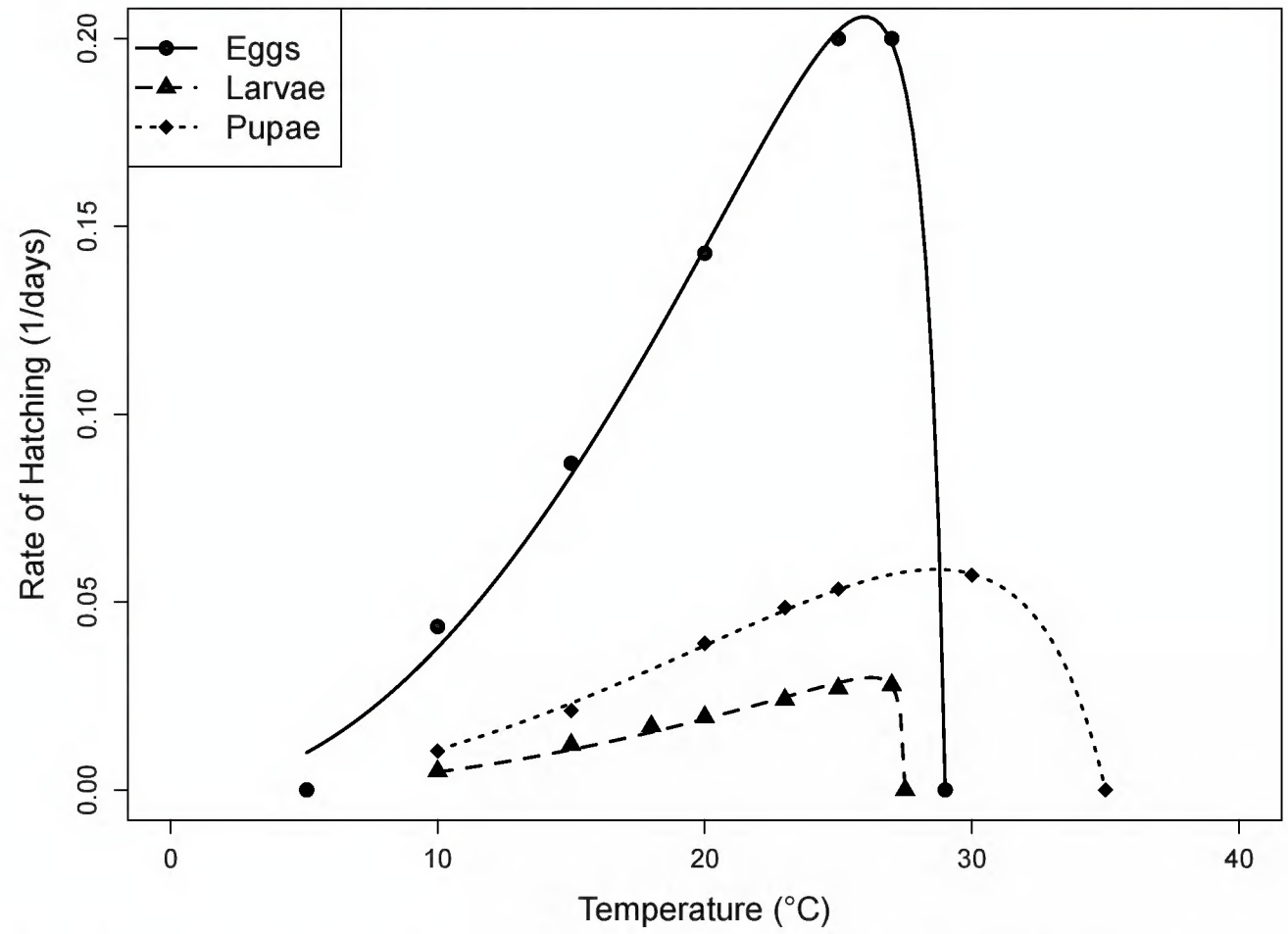

Figure 1. Fitted thermal performance curves for development rate with temperature for *Noctua pronuba* eggs, larvae, and pupae. Points indicate the data used to fit the curves.

Phenology

The phenology of the moth was described from an open insectary in Rothamsted, England, in 1961 (Table 5; cf. Madge 1962). This indicates the diapause of the pre-pupal stage and the flight stage of the adults. There is no implementation of this in the model, as it is an emergent property of the other mechanisms and part of the calibration exercise. However, the table provides helpful information to inform some of the mechanisms, for example, reproduction and longevity. It should be noted that phenology likely differs among different parts of the distribution range of *N. pronuba*. However, the UK adult flight period described by Madge (1962) mirrors contemporary patterns in Sweden, the UK, and Switzerland (e.g., Pettersson 2011; Fig. 2). Currently, we have not adapted the model to a more southerly range with warmer temperatures, where it is possible that temperature may influence the proportion of adults that enter a summer diapause (cf. Novák and Spitzer 1975).

Foraging and activity

Larvae

An investigation of the behavior of *N. pronuba* larvae in relation to light and temperature (Madge 1964b, 1964a) identified different activity patterns. First-instar larvae were active during the day (diurnal), while instars III to VII

Table 5. Phenology of *Noctua pronuba* in Rothamsted, England, during 1961, after Madge (1962). + = activity, ++ = major activity.

Stages of development	J	F	M	A	M	J	J	A	S	O	N	D
Egg								++	++	+		
Instar I									++	+		
Instar II									++	+		
Instar III										++		
Instar IV										++		
Instar V										++	+	
Instar VI											++	++
Instar VII	+											++
Pre-pupa	++	++	++	++	+							
Pupa					++	+						
Adult						+	+	++	++	+		

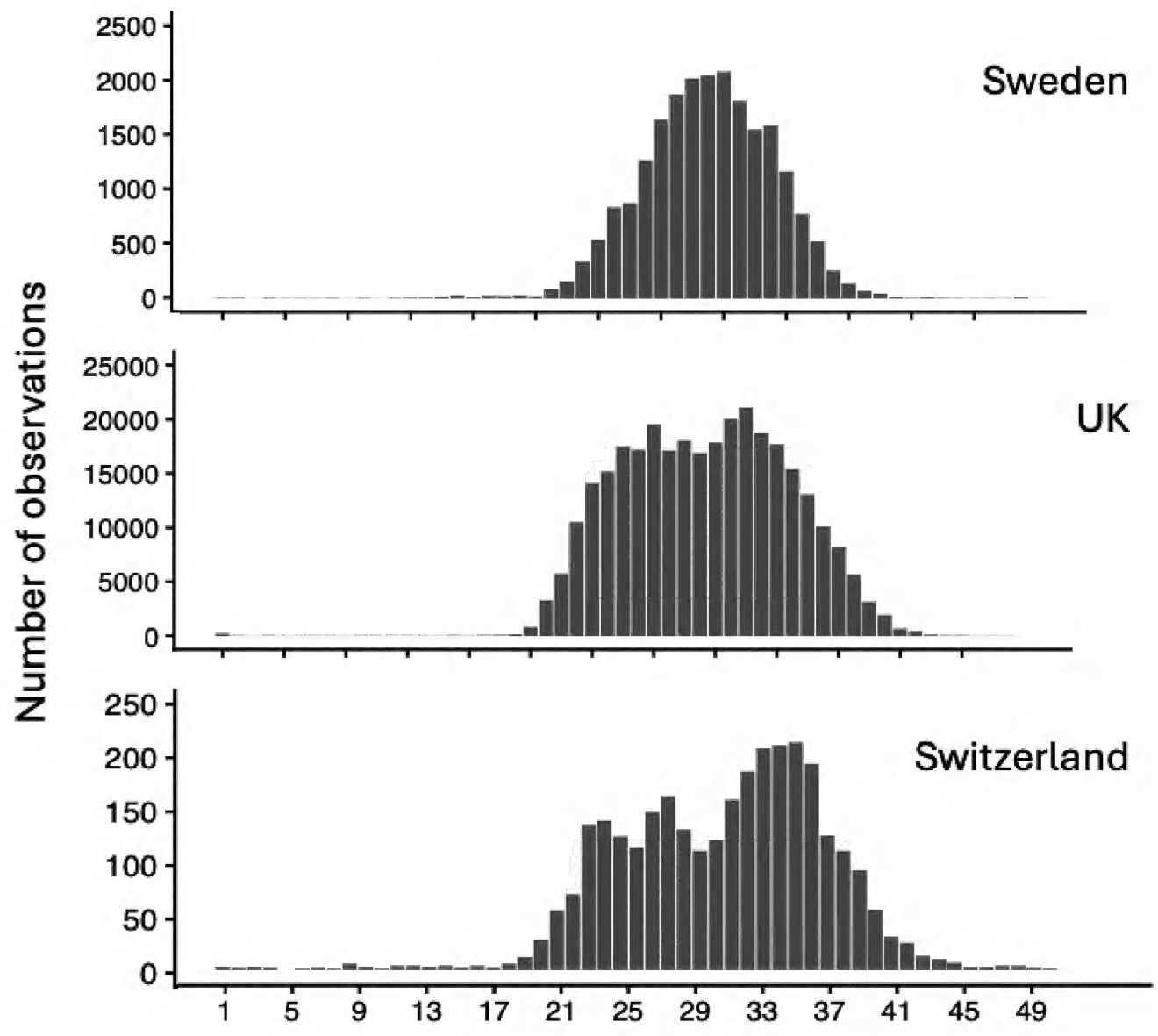

Figure 2. Phenology of *Noctua pronuba* for Sweden, Great Britain, and Switzerland during 2014–2024, shown as the number of reported observations per week during the period. GBIF Occurrence Download https://doi.org/10.15468/dl.ugcfss, accessed from R via rgbif on 2025-10-16. Adult emergence, according to Madge (1962; cf. Table 5), is approximately week 22.

were primarily active at night (nocturnal). Instar II larvae showed intermediate behavior, being somewhat active during both day and night. Thus, the entry of instar I larvae into the soil is associated with a decrease in light and a drop in temperature. For instars III to VII, activity was mostly unaffected by tempera-

ture changes but was closely related to the absence of light, indicating that these later instars prefer to be active in complete darkness, even avoiding moonlight. This may have consequences for pesticide exposure, since overspray is less likely during dark hours. Singh (1956) noted that larval instars I–VII were active on the surface of the ground, but that larval stage VII burrowed into the top layers of the soil, which may confirm Madge's observation that this stage strongly avoids light.

Adults

Heinrich (1975) reviewed the literature on insect energetics, providing information particularly relevant to Sphingidae. He calculated that a sphinx moth of 2.0 g requires 30 cal to warm up from 15°C, equivalent to the energy expended during approximately 3.7 min of flight, and that sphinx moths have a metabolic rate during flight that is near 60 mL O_2 $(g\ hr)^{-1}$. Jones (2014) measured the weight of *N. pronuba* after feeding as 0.48 g and after flying the maximum distance in a flight mill as 0.38 g. Casey and Joos (1983) showed that, despite differences attributed to physiological characteristics, these energy equations are generally transferable between moth types. Using this information, we can estimate a flight expenditure of $60 \times 0.48 / 2.0 = 14.4$ mL O_2 $(g\ hr)^{-1}$, assuming that sphinx moth energetics can be directly translated and scaled to weight. Heinrich (1975) calculated that a 3 g moth would expend 11 cal per minute of flight. Scaling for size suggests that *N. pronuba* should use approximately 1.76 cal per minute of flight.

There is a suggestion (Heinrich 1975) that foraging moths use trapline foraging, that is, repeated sequential visits to a series of feeding locations, similar to bumblebees (Buatois and Lihoreau 2016). However, this strategy is typically associated with central-place foragers. Given the high mobility of this species, central-place foraging appears unlikely, although data from mark-release-recapture experiments (Merckx et al. 2009; Slade et al. 2013) indicate that *N. pronuba* and other noctuid moths have home ranges and revisit patches that are hundreds of meters apart. However, currently there is no firm evidence to determine the foraging strategy employed by *N. pronuba*.

Implementation in the model

Larvae

We assume that feeding larval stages 1–6 are present on the surface of the soil at night, while larval stage 7 is located beneath the top layer of soil. We assume that, unless vegetation is removed by management, food is available (see Table 6 below); hence, the function of larval growth is purely to determine susceptibility to management as well as pesticides (see Mortality). We will assume that seventh-instar larvae are not affected by above-ground operations (e.g., harvest). Whether instars 1–6 are affected depends on the light levels; if the simulation time falls between dusk and dawn and the temperature is above a thermal minimum, they are assumed to be active above ground. At other times, they are assumed to be in the soil.

Adults

We assume that the 21% (0.1 g) decrease in weight after long flights in the flight mill (Jones 2014) corresponds to the maximum free energy reserves within the adult's body. In *Pieris napi*, nectar sources of 31–39% sucrose were assumed (Topping and Duan 2025). A 35% (w/w) sucrose solution has a density of approximately 1.158 g/mL at 20°C. Since Volume = Mass / Density, 0.1 / 1.158 ≈ 0.0863 mL or 86.3 µL. We can therefore assume that an actively foraging moth can consume 86.3 µL of nectar per day. In addition to flower nectar, moths feed on other sugary substances, such as ripe fruits, honeydew, and the outflowing sap of plants (Norris 1936).

Given the lack of information about a clear foraging strategy for nectar, we will assume that the moths use a foraging strategy that collects nectar of suitable concentration from local plants, moving with a directed random walk toward high nectar concentrations. We have no way to determine how much time a moth spends in each patch nor what triggers movement among patches; therefore, a stochastic neutral model was used. The amount of forage collected is assumed to follow a broken-stick model (MacArthur 1957). The number of segments of the "stick" can vary between a minimum (1) and a maximum. Currently, we have no basis for determining a maximum value, but five may be assigned arbitrarily until more information on the foraging strategy becomes available. The maximum distance travelled during foraging will be determined by the dispersal function.

Reproduction

Spitzer et al. (1984) investigated the relationship between fecundity and population fluctuations in 29 temperate noctuid moth species (Table 6). Their research provides valuable data on egg production and its ecological implications, helping to identify the range of egg-laying capacities in noctuids. The study also includes information about food-plant preferences. Combined with data from the HOSTS database (https://data.nhm.ac.uk/dataset/hosts), species were categorised based on their primary food-plant types: herbaceous vegetation (H), grasses (G), or woody plants (W).

Among the univoltine moths studied, *N. pronuba* exhibited the highest predicted population growth rate, surpassing even the cabbage moth (*Mamestra oleracea*), a species classified as a major pest (Spitzer et al. 1984).

For lepidopteran pollinators, some resources required for reproduction derive from energy stores accumulated from leaves consumed during larval feeding. Some moths rely entirely on these reserves, while others may lay a few eggs without feeding but have greatly reduced life spans and reproductive potentials unless they feed (Heinrich 1975). We assume that *N. pronuba* falls into the latter category, but there does not appear to be sufficient evidence for a food-related limit on egg production.

Studies focused on *N. pronuba* provide detailed information on reproduction. *N. pronuba* has a preoviposition period that lasts on average 58 (±8) days for larvae under temperature-controlled conditions, but adults emerging from larvae experiencing summer conditions had a preoviposition period of no less than 30 days (Singh 1956). Summer diapause (Saulich and Musolin 2017) has been

observed in several noctuid moths (Novák and Spitzer 1975), and it has been suggested that photoperiod may control its timing in *N. pronuba* (Novák and Spitzer 1975) and other species (Funakoshi 1997). Novák and Spitzer (1971) estimated that in *N. pronuba*, the critical photoperiod for ovarian activation is 15 hours of daylight, after which the moths become active. Prior to this period, there was minimal wing damage in both sexes.

Singh (1956) found that each egg cluster laid by females usually consisted of 200–300 eggs; the maximum number recorded in one cluster was 850, and the minimum was 75. Total fecundity averaged 1,014 eggs with a range of 675–1,680. The life span of adult females was 60–120 days, including a 30–70 day aestivation period. This suggests an active reproductive period of 30–50 days, assuming aestivation length was correlated with subsequent lifespan. From Table 5, we can see that the adult stage was recorded as occurring from June to October. Assuming a mid-month to mid-month period, this aligns with the 120 days noted by Singh (1956).

Madge (1962) found similar results. On average, isolated females laid about 1,371 eggs in the laboratory, while those in breeding cages laid around 1,471 eggs. Eggs were laid in 3–5 batches of 180–522 eggs after a preoviposition period of 16–24 days, which, although shorter, may correspond to the aestivation period described by Singh.

Staudacher et al. (2015) studied *Heliothis virescens*, a noctuid with a very similar egg-laying capacity and period to *N. pronuba*. They concluded that there was a trade-off between expected lifespan and egg production rate, such that moths increased egg production when diseased at the expense of oviposition site selectivity. In *Lymantria dispar*, site selection is based on proximity to forest habitat (Liebhold et al. 2008), but currently there is little information to determine whether *N. pronuba* has a specific site-selection strategy and, if so, what it might be beyond identifying appropriate larval food plants.

There is evidence suggesting different patch-size responses in visual searchers, such as diurnal butterflies, and olfactory searchers, such as nocturnal moths. Density–area relationship slopes were, on average, positive for moth species and negative for butterfly species. This should mean that most butterflies reach higher densities in small patches, whereas most moth species reach higher densities in large patches (Hambäck and Englund 2005; Hambäck et al. 2007). If we make the assumption that *N. pronuba* follows this pattern, then patch size should be included as a factor in habitat selection for oviposition.

Implementation in the model

We assume the mean day length required to trigger the start of reproduction is approximately 15 hours, but that each individual moth has its own value, drawn from a Gaussian distribution ranging from 14.5 to 15.5 hours. Once reproduction begins, the minimum lifespan is set to 30 days, but the actual lifespan is variable such that, under UK weather conditions for 1961, the model would result in a peak of adult activity during August and September and would end before November (Table 5; cf. Madge 1962). Given that we assumed weather-dependent activity, the effective lifespan is measured in active days and is therefore shorter than lifespans measured in the field. As a consequence, poor weather for activity would shift the phenology curve to the right. Final values for

Table 6. Noctuid moth species with egg production data, with added vegetation food-plant categories and pest status after Spitzer et al. (1984). The table is sorted alphabetically within subfamilies. Food categories: H = herbaceous vegetation, G = grass, W = woody vegetation. Flight distance ± 1 S.E., where available, from Jones (2014). Systematics follow Keegan et al. (2021).

Species	Subfamily	Egg Number Spitzer	Egg Number cited by Spitzer	Generations	Population Growth Rate	Coefficient of generation-to-generation variation	No. of feed plant families and category	Pimm's β	Pest Status	Flight distance (m)
Autographa gamma	Plusiinae	1180	500–2100	2	12.76	0.87	>6 H	0.07	Major	5156 ± 1064
Diachrysia chrysitis	Plusiinae	143		2	8.53	0.78	>6 H	0.37	Minor/No	
Agrochola litura	Noctuinae	201		1	4.61	0.79	4 W	0.82	Minor/No	
Agrochola lychnidis	Noctuinae	430	150–200	1	5.37	0.99	4 W	-0.48	Minor/No	
Agrotis exclamationis	Noctuinae	563	700–1200	1	5.65	0.68	>6 H	0.62	Moderate	6487 ± 1210
Agrotis ipsilon	Noctuinae	1680	1000–2500	2	13.47	2.08	>6 H	0.5	Major	
Agrotis segetum	Noctuinae	1240	300–2905	2	12.86	2.16	>6 H	0.4	Major	
Amphipoea fucosa	Noctuinae	215		1	4.68	0.86	2 G	0.84	Minor/No	
Apamea monoglypha	Noctuinae	1631		1	6.7	1.15	1 G	0.16	Minor/No	8930 ± 700
Apamea ophiogramma	Noctuinae	92		1	3.83	0.57	2 G	0.79	Minor/No	
Cerapteryx graminis	Noctuinae	310	200–500	1	5.04	0.9	1 G	0.6	Minor/No	
Denticucullus pygmina	Noctuinae	105		1	3.96	0.76	1 G	1.37	Minor/No	
Helotropha leucostigma	Noctuinae	123		1	4.12	0.86	3 H	0.77	Minor/No	
Hoplodrina octogenaria	Noctuinae	126		1	4.14	0.54	4 H	0.21	Minor/No	2364 ± 825
Hydraecia micacea	Noctuinae	180		1	4.5	0.55	>6 H	1.26	Moderate	2842 ± 864
Lacanobia oleracea	Noctuinae	1125	1000–1500	1	6.33	1.11	>6 H	1.15	Major	5042 ± 1132
Mamestra persicariae	Noctuinae	1000	1000	1	6.21	0.91	≥6 H	0.63	Minor/No	
Mythimna impura	Noctuinae	137		1	4.23	0.66	2 G	0.39	Minor/No	1460 ± 356
Mythimna pallens	Noctuinae	198		2	9.19	0.76	1 G	0.28	Minor/No	2460 ± 505
Mythimna pudorina	Noctuinae	145		1	4.28	0.53	2 G	1.04	Minor/No	
Mythimna turca	Noctuinae	305		1	5.03	0.75	1 G	0.07	Minor/No	
Noctua pronuba	Noctuinae	1960	2000–4000	1	6.89	0.94	>6 H	0.65	Moderate	11615 ± 1035
Ochropleura plecta	Noctuinae	204		2	9.25	0.85	>6 H	0.22	Minor/No	606 ± 163
Orthosia cruda	Noctuinae	231		1	4.75	0.76	5 W	0.47	Minor/No	
Orthosia gothica	Noctuinae	340		1	5.14	0.74	>6 W	0.69	Minor/No	
Orthosia incerta	Noctuinae	378		1	5.24	0.86	5 W	0.94	Minor/No	
Tholera decimalis	Noctuinae	308		1	5.04	0.55	1 G	0.56	Minor/No	
Xestia c-nigrum	Noctuinae	1430	800–1715	2	13.14	1.43	>6 H	0.58	Minor/No	5876 ± 701
Xestia ditrapezium	Noctuinae	238		1	4.78	0.86	>6 H	0.04	Minor/No	

both Gaussian distributions will be calibrated when the model is fully operational using the currently available phenology and location data.

We have no information concerning what drives the number of eggs produced by a female. However, a review of the ecology of *Heliothis* species suggested that fecundity is influenced by temperature, humidity, and larval and adult nutrition and is positively, though weakly, linked to body size (Fitt 1989). Assuming the temperature is high enough for activity, there does not appear to be a clear predictor of egg numbers in *N. pronuba*. Therefore, we will assume

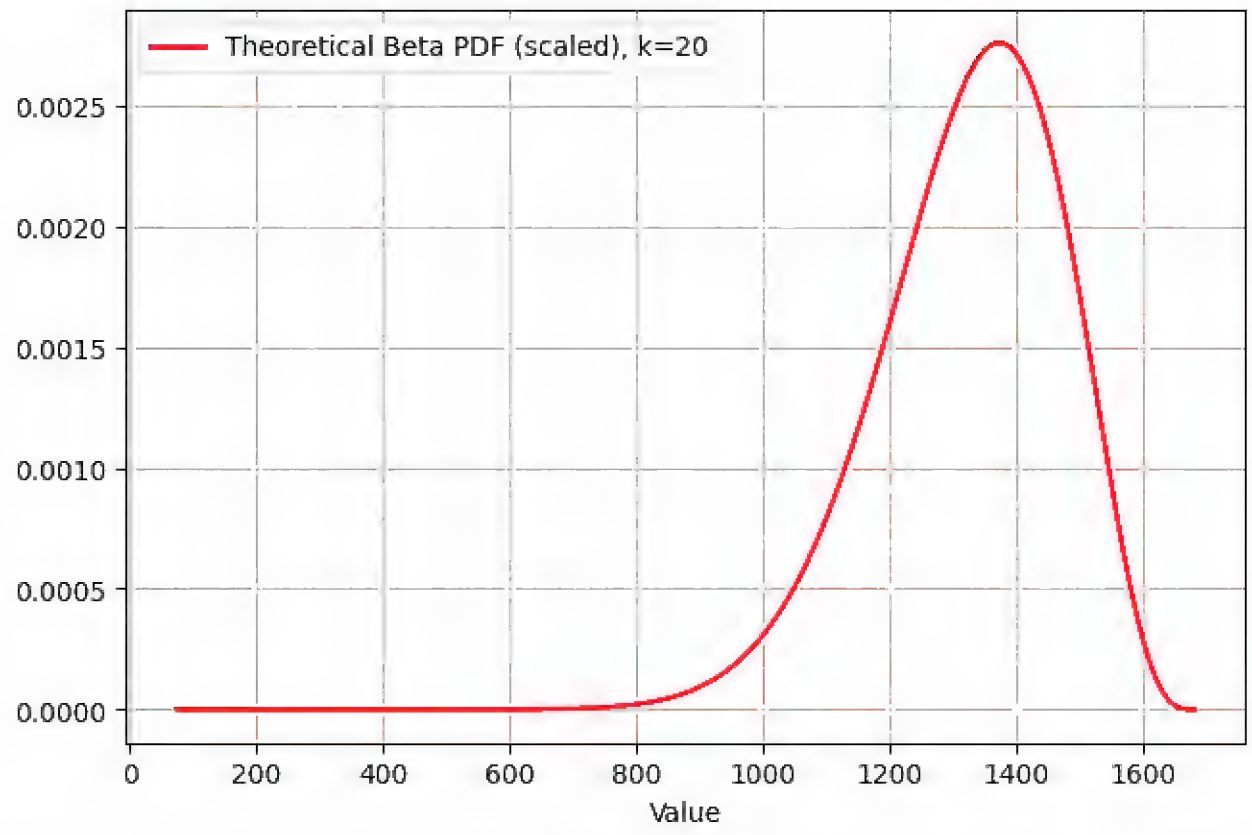

Figure 3. A skewed beta distribution fitting the criteria for the observations of maximum egg laying (a = 15.55, b = 4.449).

that each moth is allotted a total number of eggs it can produce, drawn from a skewed beta distribution with a mean of 1,323 (the average of the three results) and a maximum and minimum of 1,680 and 75, respectively (Figure 3). The value of k = 20 is arbitrary but constrains 97% of the values to fall between 1,000 and 1,600, which seems reasonable based on the observations in the literature.

To determine the number of eggs and egg batches, we will use the broken-stick model with the following modifications: the maximum and minimum number of eggs per segment must be 850 and 75, respectively, and the number of segments (egg batches) must be 3–5, or 1 if the total egg number is below 225. This method reflects the observations but provides no mechanistic explanation, which would require additional information.

Regarding oviposition location, we can assume that the moth selects suitable herbaceous vegetation within its normal dispersal range and oviposits there. Suitable vegetation can be defined as any herbaceous vegetation except that found in arable and rotational grassland fields. The probability of selection should be linearly related to the polygon area, assuming a maximum area of A (e.g., 1 ha), corresponding to maximum attractiveness. Hence, oviposition site selection should be based on stochastic probability among all polygons with suitable vegetation, scaled to size, for those below A.

If more detailed information becomes available or it is determined that cropped areas of fields can be utilised, they can be added based on vegetation type. In this way, flexibility is maintained to model other species with different host-selection behaviours.

Adult dispersal

A study by Jones et al. (2016), see also Table 6 and Jones (2014), investigated dispersal characteristics in noctuids using a flight mill (Fig. 4). Flight distances ranged from 626 m for *Ochropleura plecta* to over 12,000 m for *Amphipyra pyramidea*. Notably, *N. pronuba* achieved a flight distance exceeding 11,000 m, placing it at the upper end of dispersal potential. For species included in both

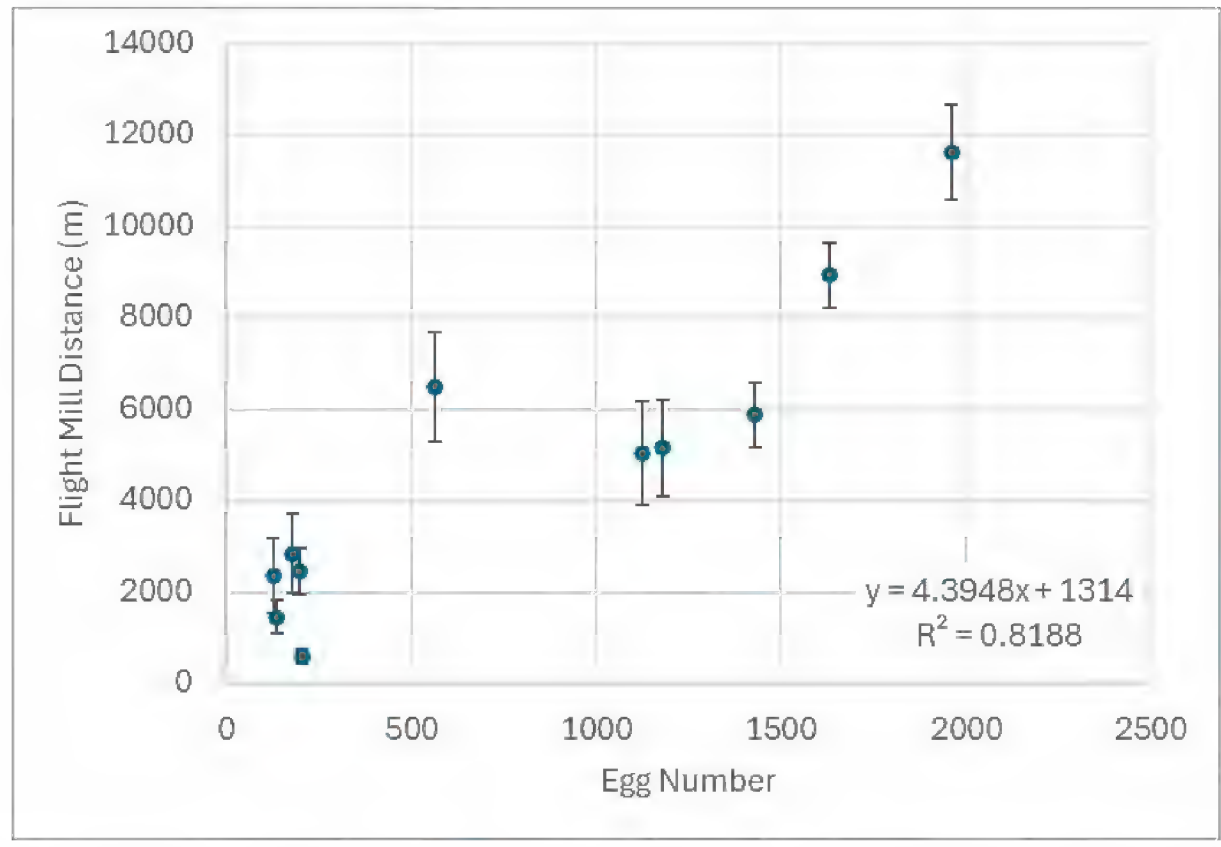

Figure 4. Noctuid flight distance plotted against egg production.

Spitzer et al. (1984) and Jones et al. (2016), correlations between flight distance and fecundity measures were explored. The only significant relationship was between egg number and flight distance, which showed a strong positive correlation (Pearson correlation $r = 0.905$, $p < 0.001$). Jones et al. (2016) noted that, while flight-mill measurements do not reflect dispersal under natural conditions, they likely represent a reliable maximum dispersal potential. The observed correlation with egg number suggests the potential for organising noctuid species along a gradient of fecundity and dispersal ability within each food-plant category. Hence, the model's design incorporates the flexibility needed for easy modification to represent other species.

Mark-release-recapture studies quantifying the daily movement of a range of noctuid moths provide model-based predictions of *N. pronuba* movement over 7 days of 472 m (Merckx et al. 2009; Slade et al. 2013). Field data for *N. pronuba* indicate a mean movement of 867 m between recaptures (N = 721 marked, range 0–2,740 m; Slade et al. 2013). The spatial distribution of recaptures by *N. pronuba* and other moths in mark-release-recapture trap networks (Merckx et al. 2009) demonstrate that several of the noctuid moths in Table 1 forage at a landscape scale, revisiting patches that are many hundreds of meters apart. While there are no studies quantifying daily movement patterns in moths, estimates for butterflies (Ovaskainen et al. 2008) likely provide a reasonable baseline, including tracking habitat edges, exploring habitat, and occasionally venturing beyond the usual patch network.

It should also be noted that flight capability in *N. pronuba* is robust, supported by navigation and migratory behaviour (Sotthibandhu and Baker 1979; Dreyer et al. 2018), although the contribution of migration is likely minor in most parts of Europe (Novák and Spitzer 1971), but see Dreyer et al. (2018). It is frequently and nocturnally active during the summer months, with inferences from related species suggesting similar flight capabilities within Noctuidae (cf. Nieminen 1996; Betzholtz and Franzen 2011).

Passoa and Hollingsworth (1996) demonstrated that the rate of expansion of invading *N. pronuba* in the USA was approximately 80 miles per year (129 km). This could be achieved in 12 days by a moth flying 11 km per day in a given direction;

alternatively, given a lifespan of 50 days (see Reproduction above), it could occur through daily dispersal of 2,580 m. Because temperature and inclement weather reduce the number of days of activity, we can deduce that the average daily dispersal distance must be upward of 2,580 m for at least some moths. However, we do not know the distribution of dispersal distances within the population nor the frequency of dispersal events, although this has been studied in some butterflies (e.g., Brown and Crone 2016). Flight capabilities are clearly well developed, as reports of attraction to light in large numbers suggest the ability to move freely.

Implementation in the model

Given the evidence of relatively large-scale adult moth movement within the 10 × 10 km range of typical ALMaSS landscapes, we may assume that dispersal, when weather is suitable, is not a limitation for finding food or reproductive locations. Thus, we will assume that dispersal distances are up to 11 km; hence, with wrap-around boundaries normal in ALMaSS, dispersal distance will not hinder movement toward food or reproductive sites, but it will limit movement between days. If we assume that the daily dispersal distance is drawn from a Gaussian distribution varying from *D*min to *D*max, where *D*max is 11 km and *D*min is 100 m, then this will simulate the situation for *N. pronuba*. This also allows *D*max and *D*min to be changed to simulate other species.

Whether dispersal—and therefore foraging and reproduction—can occur will depend on weather conditions. We assume that a minimum temperature is required for activity. Temperature effects on moth activity are well documented (e.g., Williams 1940; Williams 1961). While activity is often influenced by the preceding temperature rather than absolute values (Williams and Buxton 1951), low temperatures reduce activity. The influence of precipitation or high wind velocities is less clear, and there may be substantial moth activity even during rainfall and strong winds, and effects may interact with temperature (Esbjerg 1987; Neff et al. 2025). Williams (1940) emphasises the importance of season for moth activity; rainfall can substantially lower moth activity in summer but has negligible effects in winter. Temperature changes, on the other hand, have strong effects in winter but can be neglected in summer.

Mortality

Parasitoids and other biological agents

Summarising Singh (1956), the main sources of biotic mortality for *N. pronuba* include bacterial and viral infections; parasitism by various Ichneumonidae, Braconidae, Tachinidae, and Bombyliidae species; predation by carabid beetles such as *Pterostichus madidus*; and vertebrate predators, including birds, bats, and rodents (Tinbergen 1981; Mikula and Cmokova 2012; Lindstedt et al. 2019). Cannibalism among larvae is also a significant mortality factor, particularly under crowded conditions. It should be noted that many of these observations derive from captive populations and may not be directly transferable to wild population dynamics.

In addition to what is known about *N. pronuba*, data for other moths indicate additional parasitoid species and genera that could be important, such as *Pales pavida* and *Ramonda spathulata* (Tachinidae) (Ford and Shaw 1991),

and Trichogrammatidae, such as *Trichogramma cordubensis* (Roriz et al. 2006). *Microplitis mediator* (Hymenoptera, Braconidae) is a major cause of mortality for the cabbage moth (Belz et al. 2014), and Braconidae such as *Cotesia marginiventris* exhibit Type II functional responses to *Spodoptera* larvae (Riggin et al. 1994). *Beauveria bassiana* is a mortality factor for multiple noctuid pests (e.g., Hicks et al. 2001; Mantzoukas et al. 2013; Apirajkamol et al. 2023), and microsporidia and viruses also contribute to mortality pressure (e.g., Hamm and Lynch 1982).

Taken together, these multiple mortality sources—with their potential for rapid buildup—suggest that, in all these species, density-dependent mortality may occur at high densities due to parasitoids, diseases, and cannibalism. However, it is difficult to determine the rates or density thresholds due to the variability in mortality levels among species and locations.

Implementation in the model

The literature does not provide a clear picture or sufficient data to support the development of a specific mortality model. We therefore propose adopting a spatially explicit model representation at two levels. For high densities, an area-based modifier to mortality chance per day will simulate increased direct density-dependent mortality by transmissible diseases and cannibalism. In addition, a parasitoid model of the type suggested for *Pieris napi*, using an agent-based representation, would provide a time-delayed spatial density-dependent function. Since these will be implemented in a general manner, calibration against time series of real data will be necessary during the calibration phase.

In the *P. napi* model (Topping and Duan 2025), the parasitoid population is simulated using a spatially explicit agent-based model tracking individual life histories. The core reproductive behavior follows a functional response combining search efficiency and handling-time constraints:

$$E_{\text{laid}} = \min\left(E_{\text{remaining}}, \frac{D}{T_h + \frac{1}{H \cdot S_e \cdot T_s}}\right) \qquad \text{Equation 2}$$

where $E_{\text{remaining}}$ is the remaining egg complement, D is daylength, T_h is handling time per host, H is host density, S_e is search efficiency, and T_s is searching time. Individual agents disperse spatially to locate hosts, with development, emergence, and overwinter survival governed by temperature and photoperiod thresholds as described in the model documentation. Superparasitism by different individuals was permitted.

We assume the non-parasitoid density-dependent mortality will follow Equation 3:

$$m(d) = m_0 + a d^{\beta} \qquad \text{Equation 3}$$

Where $m(d)$ is the daily mortality rate at density d, m_0 is the baseline mortality rate (density-independent), a is a scaling coefficient, β is the density exponent (typically $\beta > 0$ for density-dependent mortality), and *d* is the local density (e.g., individuals per hectare). Mortality rates, thresholds, and areas over which density dependence operates will all need to be calibrated.

Pesticide responses

As with *Pieris napi*, we follow the basic approach used in the development of the ApisRAM honey bee colony model (Duan et al. 2022). Pesticide exposure can occur through the consumption of contaminated nectar, contact, and overspray. By considering these three exposure pathways, we represent how model moths may encounter pesticides in contaminated environments. $P_B(t)$ is used to represent the accumulated pesticide burden for the individual until day t. $P_B(t)$ is updated by all three exposure paths and is used to calculate the stress caused by pesticide exposure. The new pesticide exposure on day *t* is represented by $P_N(t)$, which is calculated by Equation 4.

$$P_N(t) = P_I(t) + P_C(t) + P_O(t) \quad \text{Equation 4}$$

where $P_I(t)$ is the new contamination from intake, $P_C(t)$ is from the contact exposure, and $P_O(t)$ is from the overspray exposure.

Intake exposure pathway

This pathway accounts for pesticides that larval and adult moths ingest. Foraging moths may be exposed by collecting nectar from contaminated flowers, while larvae may eat contaminated leaves. The pesticide amount in the consumed resource is represented by $P_I(t)$ and is assumed to move directly into the moth's body ($P_N(t)$).

Overspray and contact exposure pathways

The overspray exposure pathways are relevant only to any moth life stage present at the moment of pesticide spraying. Contact exposure can occur when a mobile stage moves through a contaminated area. In both cases, a simple one-time absorption model is used, meaning we assume that the pesticide is absorbed into the moth's body only once, controlled by separate parameters for contact and overspray.

Contact exposure specifically pertains to foraging adults and larvae and occurs when a moth touches a contaminated surface during its foraging activities. The amount of pesticide transferred to the body through contact is controlled by two user-defined parameters, as shown in Equation 5.

$$P_C = s_c S P_s \quad \text{Equation 5}$$

where P_s is the pesticide amount per square meter on the plant surface, S is a constant representing the area of the moth in contact with the surface (for adults, this may include the feet, abdomen, and wings), and s_c is the absorption rate that determines how much of P_s is transferred to the body. This implementation does not account for foraging time, but both parameters can be adjusted to make the approach more or less conservative.

Overspray occurs only when moths are active or resting (adults or larvae) in a field where pesticide spraying is taking place and/or where drift is occurring in an adjacent area containing the moths. Two parameters—starting time

and ending time—determine whether overspray can occur. Overspray can occur only if a moth is in the exact location and not protected from the spray (e.g., not in the soil). When overspray occurs, the contaminated pesticide amount (P_O) entering the moth's body is calculated using Equation 6.

$$P_O = s_o S a \qquad \text{Equation 6}$$

where S represent a proportion of the body surface, a is the pesticide spraying application rate, s_o is the absorption rate for overspray.

Toxicology

To determine the effect of pesticide body burden, the initial model considers only acute mortality. This approach requires three parameters: first, a threshold for effect (P_t) above which mortality occurs; second, a daily probability of mortality (P_m) when the threshold is exceeded; and third, a daily decay rate (D) of the pesticide in the moth's body. This provides a first-stage model for evaluating pesticide effects and assumes that an ALMaSS or equivalent landscape model is available to generate pesticide concentrations in nectar, vegetation, and overspray.

Other mortalities

These are mortalities not specifically modelled above and include random predation events, mortalities as a result of management (e.g., ploughing (Badenes-Pérez 2022)), and "catch-alls," which simply prevent exceedingly long lifespans, which could result from applying probabilities. Here we consider mortality related to soil moisture, temperature, and management events.

Temperature-related mortality: assumes that life-stage survival at temperature *T* is the result of exposure to a constant daily jeopardy that is a function of temperature. Under variable conditions, this can be represented by Equation 7:

$$S_t = \prod_t \gamma(T_t, \boldsymbol{C})^{\Delta t} \qquad \text{Equation 7}$$

Equation 7 describes the overall survival probability of an insect's life stage under variable temperature conditions. It states that the survival probability *S*t over a given time period is the product of daily survival probabilities $\gamma(T_t, \boldsymbol{C})$ raised to the power of the time step (Δt). This means that the survival probability for each day (or fraction of a day) is calculated based on the temperature for that day, and these daily probabilities are multiplied together to get the total survival probability over the entire period. $\boldsymbol{C}$ is a vector of parameters, for example, representing a polynomial function.

Implementation in the model

Implementing Equation 7 will have the advantage of including temperature-induced variation in background mortalities associated with functions not specifically addressed in the model. This is typically represented as a fixed daily mortality, but here, we propose that the daily mortality should be adjusted using Equation 7 and replaced by $S_t Bs$, where *Bs* represents the stage-specific daily

survival chance as a constant, calculated daily from the daily mean temperature (T). Régnière et al. (2012) used a second-degree polynomial in a logistic model to represent *Choristoneura fumiferana* larvae survival with temperature as $\gamma(T_t, \boldsymbol{C})$, and this seems a reasonable choice given we have no equivalent data set for a suitable noctuid species, Equation 8:

$$\gamma = 1/(1 + exp(a + bT + cT^2)) \qquad \text{Equation 8}$$

Singh (1956) provides information for larval survival at different temperatures, which can be used to parameterise the curve. Although not comprehensive, the data suggested optimal survival at 15–20°C and no development below 5°C, with no increase in mortality observed either. At 10°C, mortality was 90%. At 25°C, 7% of the larvae survived, and almost 100% died at 27.5°C. We must assume that either the 5°C or 10°C values are correct. Given that no larvae survived at 5°C, we will assume the value at 10°C is correct. However, at optimal development, 50% of the larvae also died; thus, to fit the curve, which must range from 0 to 1.0, it was fitted with 20, 14, and 0% survival at 10, 25, and 28°C. The values from the study are confounded by the length of development, which means that the actual survival chance per day needs to be calculated based on the developmental time predicted by Equation 1. This was done by raising the survivorship by the power of the development time for that day and then fitting the curve.

Equation 8 provides a survivorship probability of the form shown in Fig. 5, with $\boldsymbol{C}$ (a = −22.33, b = −4.0, and c = 0.119). The final values for $\boldsymbol{C}$ and βs will be determined during the calibration stage of the final model.

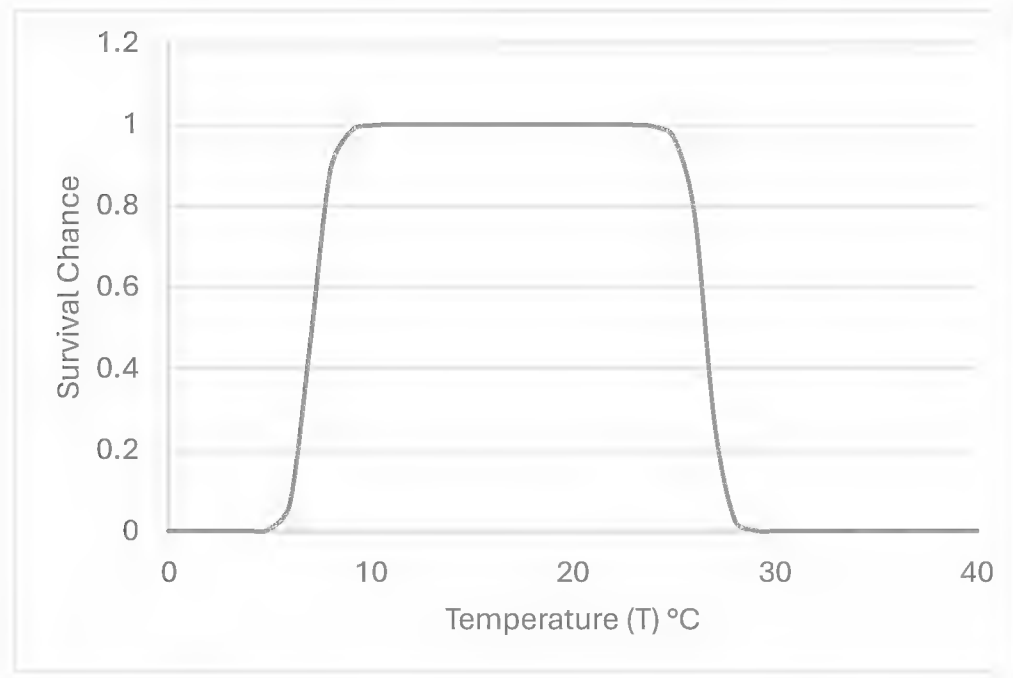

Figure 5. Survivorship probabilities from a 2nd-order polynomial in a logistic equation (Equation 8).

For the eggs, the following summary comes from Madge (1962) for *N. pronuba*:

- **Egg development at constant temperatures:** The study found that egg hatching was highly temperature-dependent. Mortality rates increased significantly at temperatures above 27°C, reaching 100% at 29°C. Newly hatched larvae at these higher temperatures had very low survival rates.
- **Egg development at alternating temperatures:** Eggs kept at alternating temperatures exhibited a higher hatching percentage compared to those maintained at a constant temperature of 10°C.

- **Sub-threshold temperatures:** Eggs incubated at very low temperatures (5°C and 0.8°C) did not hatch but showed some development. After being moved to a higher temperature (25°C), a portion of these eggs were viable, but none hatched after 4 to 5 weeks at the low temperatures.
- **Semi-natural conditions:** In a semi-natural setting, nearly all eggs hatched after 12 to 13 days at a mean temperature of around 14°C. However, when the temperature dropped below 5°C, only 4% of the eggs hatched after 5 weeks, indicating that lower temperatures significantly hindered development.

Unfortunately, more detailed data on egg survivorship were not presented; however, the data provided suggest that the pattern is quite similar to that of the larvae (see above). Therefore, the same type of curve was fitted with the constraints that mortality should reach 100% at 5°C and 100% at 29°C, with "high" mortality at 27°C. Non-zero values were needed to allow fitting, so the curve was fitted with 5% survivorship at 6 and 28°C. The resulting parameters for Equation 8, assuming the development times of eggs predicted by Equation 1, were a = 15.48, b = −4.0, and c = 0.1157, respectively.

Finally, we assume that the mortality of non-diapause stages will occur with the onset of winter (here we assume December 1st) or with negative temperatures lower than a minimum temperature threshold (Min_T), initially assumed to be −10°C, and that mortalities will also be associated with management events for juvenile stages.

Implementation in the model

We assume that all soil cultivation results in mortality for non-adult stages, initially at 100%, unless other information becomes available. Other management should be considered on a case-by-case basis when applying the model. However, since the larvae are active at night, most above-ground operations will not directly affect them. Indirectly, we might assume larvae to be affected by the total removal of green vegetation biomass. In this case, the initial assumption will be that they die. The effect of this assumption will need to be tested in the calibration phase, and if found important, it should be modified. This modification could allow movement for a period of time to find new green vegetation.

Soil moisture

From Singh (1956), we know that larvae and pupae resting in the soil require a certain soil moisture content for survival (6–8% for larvae and 4–6% for pupae), given a soil water maximum capacity of 27%. Above and below these levels, survival is reduced, with zero survival at 2% and 10% soil moisture (as a percentage of dry weight). Unfortunately, Singh did not report on egg survival, but unless other information comes to light, we can assume it is the same as for larvae.

Implementation in the model

We assume a super-Gaussian function, which provides a flattened top to a normal distribution curve. The function produces a virtually identical shape to Equation 8 but is symmetrical around the centre point (Equation 9).

$$f(x) = exp(-((|x|)/a)\hat{}\mathrm{n}) \quad \text{Equation 9}$$

Values of *a* and *n* of 3.5 and 5.6, respectively, when offset along the x-axis by 6.9% moisture, create a curve with 100% survival from 6% to 8%, and then a decrease to zero survival at 2.2% and 11.7%. This is not optimal, but if we assume this mortality probability is applied daily, it will penalie wet and dry conditions quickly. For the pupae, the same curve can be used with parameters *a* = 3.5 and *n* = 4.4. This provides optimum conditions at 4–6% moisture, with declining survivorship to zero per day at zero and 10.2% moisture. Given the limited precision of the available estimates, we believe this method will reasonably represent the situation.

Discussion

The formal model presented here aims to provide a comprehensive framework for simulating *Noctua pronuba* population dynamics within the ALMaSS system for pesticide risk assessment and as a basis for extending this approach to other similar moths. Our analysis of available literature and parameterisation efforts reveals several important insights about modelling this nocturnal pollinator species.

Behavioural and ecological complexity

We integrate a number of complex behavioural patterns, including stage-specific activity patterns (diurnal early instars transitioning to nocturnal behaviour), temperature- and light-dependent foraging, medium-distance dispersal capabilities, and photoperiod-triggered reproductive diapause. Our aim is that these features capture the ecological realism necessary for accurate risk assessment while maintaining computational feasibility within the ALMaSS framework. However, see the caveats under Framing the Model.

Pesticide exposure pathways

The three-pathway exposure model (intake, contact, overspray) accounts for the multiple routes through which moths may encounter pesticides. The distinction between larval exposure (through contaminated foliage) and adult exposure (through nectar feeding and contact) is particularly important for accurate risk assessment, as these life stages occupy different ecological niches and exhibit different behaviours.

Model limitations and uncertainties

Several areas of uncertainty remain within the current model framework. The exact nectar foraging strategy employed by *N. pronuba* remains unclear, with the current broken-stick model serving as a placeholder for more mechanistic representations. While density-dependent mortality is clearly important for population regulation, specific thresholds and rates require calibration against field data. Furthermore, the current acute mortality framework is overly simplified and would benefit from incorporating sublethal effects and chronic exposure impacts. It should also be noted that we assume *N. pronuba* toxicity can be inferred from standard laboratory tests, which may not fully capture species-specific responses.

The successful fitting of Lobry–Rosso–Flandrois TPCs to developmental data from Singh (1956) and Madge (1962) demonstrates that *N. pronuba* development follows predictable temperature-dependent patterns across all life stages. The LRF model's flexible parameters allow the representation of other noctuid species with similar ecological niches. This adaptability may be particularly valuable given the similarities in developmental patterns observed across pest noctuid species, such as *Helicoverpa armigera* and *Spodoptera frugiperda*.

However, the TPC approach used was poor for estimating the minimum development temperature, despite highly significant fits for the other TPC parameters. This result suggests that the shape of the LRF TPC does not accurately capture the response to low temperatures. This is possibly a general property of this type of TPC curve. Still, by using the curve only during the growth period and truncating it when observations show no development, we believe we avoid any serious error.

The mechanism of controlling diapause is not clear. Assuming our proposed model is correct, then in warm years this species should become bivoltine. However, this has not been definitively recorded in literature, suggesting another mechanism of breaking diapause might be in play. However, Singh (1956) quotes South (1907): "when eggs are obtained early, the caterpillars from them will sometimes attain the moth state in the same year." Thus, it is claimed that in the UK, there can be a partial second generation. The alternative mechanism suggested is adult aestivation, which would prevent a second generation by pushing the reproductive period to autumn (Novák and Spitzer 1975). On balance, we chose the temperature-controlled model for phenology but included the photoperiod-controlled adult aestivation. This does not explain the UK observation of direct development from egg to adult within a single calendar year, which does not appear to have been re-recorded subsequently.

Implications for risk assessment

This model provides several advances for pesticide risk assessment. Integration with ALMaSS enables simulation of moth populations across realistic agricultural landscapes with spatially explicit pesticide applications. The model's detailed life cycle representation enables the assessment of stage-specific vulnerabilities and exposure scenarios. At the same time, incorporating activity patterns and dispersal capabilities yields more realistic exposure estimates than static models alone. Additionally, the framework allows evaluation of pesticide impacts alongside other mortality factors and environmental stressors, providing a more holistic assessment.

Framing the model

Domain of applicability

This model is designed specifically to simulate the population-level responses of nocturnal lepidopteran pollinators to pesticide applications in temperate European agricultural landscapes. The parameterisation using *N. pronuba* data constrains its primary applicability to univoltine species with similar life histories, overwintering as larvae, and utilising herbaceous vegetation as larval hosts.

The ALMaSS framework limits the model's spatial domain to landscapes of typically 10 × 10 km, which is sufficient for capturing local population dynamics but may potentially overlook larger-scale metapopulation processes. This may be a problem for highly mobile species such as *N. pronuba* with migratory tendencies. However, our focus on local pesticide effects means we are specifically interested in within-landscape exposure and response dynamics rather than population-level persistence, making the exclusion of large-scale migration appropriate for addressing our research questions. Temporally, the model operates on daily time steps over multiple years, making it suitable for assessing both acute pesticide impacts and longer-term population trajectories but not for capturing within-day behavioural dynamics or evolutionary responses.

Key biological processes not included

Evolutionary and adaptive responses

The model assumes fixed behavioural and physiological parameters, excluding potential evolutionary adaptations to pesticide exposure or changing agricultural practices. Real populations may develop resistance, alter behavioural patterns, or shift phenology in response to selection pressures, i.e., processes that could significantly influence long-term risk assessments but operate on timescales beyond typical regulatory evaluations.

Social information and learning

While *N. pronuba* likely uses visual and chemical cues to locate resources and mates, the model treats each individual as making independent decisions. We do not include pheromone communication, aggregation behaviours, or information transfer between individuals that could influence exposure patterns. For instance, if moths avoid or are drawn to areas where conspecifics have died from pesticide exposure, actual population-level impacts might differ from model predictions.

Microhabitat selection and refugia

The model operates at a 1 m² spatial resolution, and polygons are, for the most part, assumed to be uniform. However, larvae make behavioural decisions at much finer scales. We do not capture how individuals might select specific positions on plants, exploit microclimatic refugia, or preferentially use field margins versus crop centres. These fine-scale behaviours could create spatial heterogeneity in exposure that buffers populations from pesticide impacts. They will result in variation in the effect of environmental factors, which cannot be explicitly included at this scale.

Host plant quality and preference

We do not consider diel variability in nectar production in ALMaSS. However, this is known to be a feature of some plants (Kendall and Nicholson 2025). This would alter the nectar availability as seen by nocturnal species such as *N. pronuba*. While the model includes nectar availability, it treats all suitable vegetation equally for

larval development. In reality, *N. pronuba* shows preferences in its polyphagous diet, and larval performance varies with host plant species, nutritional quality, defensive compounds, and the microclimates in which plants are growing. This simplification may overlook important dynamics in which pesticide applications interact with host plant availability, thereby creating population bottlenecks.

Sublethal and transgenerational effects

The current toxicology module primarily focuses on acute mortality; however, growing evidence suggests that sublethal pesticide exposure can impair navigation, reduce fecundity, alter development rates, and even affect offspring fitness through epigenetic mechanisms. These cascading effects could accumulate over generations in ways our single-generation mortality approach cannot capture.

Interactions with other species

N. pronuba exists within a complex ecological network, competing with other herbivores, serving as prey for various predators beyond the modeled parasitoids, and potentially benefiting from or being hindered by the activities of other species. The single-species focus misses important indirect effects. For example, pesticides might reduce *N. pronuba* populations more by eliminating their preferred larval hosts than through direct toxicity or by impacting parasitoid populations, thereby reducing mortality.

Climate variability and extreme events

While the model incorporates temperature and moisture effects on development and survival, it assumes these follow predictable daily patterns. Extreme weather events, such as heat waves, flooding, and late frosts, can cause catastrophic mortality or trigger unusual behavioral responses not captured by smooth functions fitted to laboratory data (Oliver et al. 2015). However, there is great variability in lepidopteran responses to extreme climate events (Palmer et al. 2017). Climate change may also alter the synchrony between moth phenology and resource availability in ways the current framework cannot anticipate or alter voltinism.

Mortality dynamics

The multi-faceted mortality framework, incorporating density-dependent factors (parasitism, disease, and cannibalism), temperature-related survival, and management impacts, provides a realistic representation of population regulation. The high diversity of mortality sources identified, from viral and bacterial infections to multiple parasitoid families, suggests that *N. pronuba* populations are subject to strong but variable natural control. Thus, dynamics not considered may occur in reality.

Philosophical boundaries

The model embodies several implicit assumptions about how we conceptualise moth populations for risk assessment. By emphasising population dynamics over individual fitness, the model aligns with regulatory frameworks

that typically consider population-level impacts rather than individual effects. Using TPCs implies that development is fundamentally predictable given environmental conditions, potentially missing stochastic elements that contribute to population resilience, such as interactions between health and development. The 1 m² resolution still assumes uniform conditions within each cell, philosophically treating space as discrete rather than continuous. Finally, the modular approach to mortality factors assumes that their effects combine predictably, even when synergistic or antagonistic interactions occur. This issue may be less important due to the individual-level model, but it could be a factor in within-body interactions.

Implications of model framing

These exclusions are not oversights but deliberate choices that strike a balance among biological realism, computational tractability, and data availability. For regulatory risk assessment, the model provides a tool for comparing relative risks across scenarios rather than predicting absolute population outcomes. Users should interpret the results as indicating whether pesticide applications are likely to pose population-level risks under the assumed conditions, rather than as precise forecasts of moth abundance.

The model is best suited for comparing the relative impacts of different pesticide application scenarios, identifying life stages most vulnerable to pesticide exposure, exploring how landscape composition influences population resilience, and assessing whether spatial refugia can maintain viable populations. It is less appropriate for predicting exact population sizes, evaluating pesticide impacts in non-agricultural landscapes, or predicting extinction probabilities. It would be inappropriate for assessing long-term evolutionary responses to pesticide use or for extrapolating to species with substantially different life histories.

By explicitly acknowledging these boundaries, we position the model as a focused tool for specific risk assessment questions while remaining transparent about the biological complexity that remains outside its scope. This framing allows users to apply the model appropriately while recognising that real-world moth populations may exhibit dynamics beyond what any tractable model can fully capture.

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Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

Use of AI

No use of AI was reported.

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Author contributions

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Data availability

All of the data that support the findings of this study are available in the main.

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